PAST ECOSYSTEM DYNAMICS IN FASHIONING VIEWS ON CONSERVING EXTANT NEW WORLD VEGETATION[1]

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ABSTRACT

In the Cretaceous there were eight New World terrestrial ecosystems that were distinct or only shadowy versions of those present today. Now, 65 Ma later, 12 ecosystems constitute the recognizable subdivisions of the Earth's living and physical envelope. Knowledge of the intervening history is useful for conservation in several regards. It reveals how heterogeneous modern systems are in age and origin (e.g., lowland Neotropical rainforest formed between ca. 60 and 58 Ma; tundra and páramo between ca. 5 and 3 Ma), how individualized the response of component species to previous environmental change has been, and how levels of biodiversity have fluctuated through time. History provides approximate analogs for conditions anticipated in the near future and estimates of the biotic response. In addition, history documents that climatic events originally discovered and formerly associated with the high latitudes also affected tropical regions, and that discovery constitutes a valuable context for assessing previously held views about the stability of tropical communities and environments. There has been a rapid increase in the pace of both natural and human-induced environmental change and biotic response approaching modern times. Blurring the lines between neontology and paleontology, namely, conceptualizing ecosystems over Cretaceous and especially Late Cenozoic time, provides a dynamic view of these systems and furthers realistic strategies to conserve them.

Key words: Climate change, conservation, ecosystems, New World vegetation, paleobiology.

Ecosystems are the plants, animals, physical features, and climates that interact to define recognizable segments of the landscape. Modern ecosystems in the sense of angiosperm-dominated communities started to appear in the Early Cretaceous ca. 125 million years ago (Ma), and by the end of that period (ca. 65 Ma), they had diversified and radiated to become the principal component of the Earth's living envelope (Graham, 2010a; Friis et al., 2011).

Initially in the Cretaceous there were eight ecosystems recognized for the New World: the polar broad-leaved deciduous forest, notophyllous broad-leaved evergreen forest, paratropical rainforest, tropical forest, aquatic, freshwater herbaceous bog/marsh/swamp, mangrove, and beach/strand/dune. These developed into the 12 ecosystems recognized for the present interval of time: desert, shrubland/chaparral-woodland-savanna (caatingas and cerrado), grassland (pampas in Argentina), mangrove, beach/strand/dune, freshwater herbaceous bog/marsh/swamp (including the Pantanal of Brazil, Bolivia, and Paraguay), aquatic ecosystems, lowland Neotropical rainforest, lower to upper montane broad-leaved forest (mostly mid-altitude Latin America)/deciduous forest (mostly North America north of Mexico), coniferous forest, alpine tundra (páramo), and tundra. Some appeared early and were already present in the Cretaceous, such as aquatic with representatives of Nymphaeaceae, *Ceratophyllum* L., *Decodon* J. F. Gmel., *Trapa* L., *Pistia* L., and others (Graham, 2010a [appendix 2.1, 2.2], 2011, 2011 et seq.), while others came later with increased drying and greater seasonality beginning in the Middle Miocene (ca. 15 Ma) and formed shrublands, woodlands, savannas, grasslands, and the early versions of desert. Early versions of others, such as tundra and alpine tundra or páramo, appeared even later when cool temperatures combined with increasing altitudes in the Late Miocene and Pliocene beginning ca. 6–7 Ma and became established ca. 5–3 Ma. In some instances, the physical opportunity for the development of a particular ecosystem was present in the Cretaceous (such as coastal brackish-water habitats), but the appearance of modern mangrove communities had to await the migration of *Rhizophora* L. into the New World, which did not happen until the Middle Eocene (ca. 45 Ma; Germeraad et al., 1968); oak did not cross the Panama land bridge into northern South America until ca. 330,000 years ago to form the present-day oak-*Weinmannia* L. forest of the upper Andean forest belt (Hooghiemstra & van't Veer, 1999; van't Veer & Hooghiemstra, 2000).

Biodiversity and the importance of preserving it are being widely presented to the public (e.g., Clark & Poulsen, 2012); hence the inclusion of selective

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references from the popular media (e.g., Safina & Lewison, 2014). However, the reasons for the present high levels particularly of tropical biodiversity are complex (Kraft et al., 2011), and history reveals this level is not the result of a simple straight-line increase in the tempo of evolution and the accumulation of species through time. Estimating past levels of biodiversity is an inexact science, but Wing (1997) suggested that during the warm interval around the Paleocene/Eocene boundary ca. 55 Ma, widely separated areas of North America, like the northern Rocky Mountains and the Gulf Coastal Plain, experienced a short-lived decline in diversity. Wilf et al. (2003, 2005) believe that sometime around 52 Ma there was high diversity in warm parts of South America (Patagonia, Argentina). Hoorn (1994) reported 280 pollen types in Miocene river sediments from northwestern Amazonia, while Urrego-Giraldo (1994) recovered only half that number in comparable sediments of Holocene age from the same region; Wijninga (1996) detected a decline from the Miocene into the Quaternary in Colombia. Paleobiology reveals modern ecosystems are heterogeneous assemblages of disparate communities that appeared at different times (Cretaceous through the Mio-Pliocene), originated in different ways (in situ and near–in situ evolution vs. components arriving via migration), and experienced its own complex ebb-and-flow pattern of diversity and extinction (Colles et al., 2009; Davies et al., 2011; Lorenzen et al., 2011; Uyeda et al., 2011). A summary of New World ecosystem history is given in Graham (2011; see also Graham, 1999, 2010a, 2010b, 2012; Raven et al., 2011, and papers therein). In addition to past effects, there are the numerous and widely discussed modern impacts on ecosystems (Dizro et al., 2014; Gillis, 2014; Gillis & Chang, 2014; Pimm et al., 2014; Stokstad, 2014; Vignieri, 2014) due to human activities, such as farming, lumbering, grazing, burning, and construction (Allan, 2011; Barrett et al., 2011; Doxford & Freckleton, 2011; Hoffmann & Sgrò, 2011; Kodra et al., 2011; Lee et al., 2011; Laurance, 2012a, 2012b; Laurance & Balmford, 2013). Recent studies suggest that species are shifting to higher elevations at a rate of 11.0 m/decade and to higher latitudes at 16.9 m/decade in response to global warming caused in part by increasing atmospheric CO_2 concentration (Chen et al., 2011), and that this is resulting in an Amazon basin transitioning to a disturbance-dominated regime (Davidson et al., 2012). Ecosystems will increasingly fluctuate in the future through a combination of natural factors and anthropogenic changes in the environment (SANparks, 2010) influencing the distributions, ecological tolerances, and levels and patterns of biodiversity established in the past.

Past environments, lineages, and communities can serve as useful analogs for conditions anticipated in the future and for estimations of the biotic response. Atmospheric CO_2 concentration was ca. 300 parts per million by volume (ppmv) just before the industrial revolution in the early 1800s. Currently, that concentration has grown to 400 ppmv; it is expected to increase to 550 ppmv by 2050 and reach 1000 ppmv by the end of this century. Near the end of the Cretaceous, CO_2 concentration was ca. 1500 with its equable temperatures and mesic vegetation; it was 2000 ppmv at the Paleocene-Eocene Thermal Maximum (PETM) around 55.9 Ma when tropical tapir, crocodile, and banana-like lineages extended to within the Arctic Circle. The rate of carbon emission is estimated at 300–1700 million metric tons per year (Cui et al., 2011). Current emissions are 10 times that of the PETM. Atmospheric CO_2 concentration was less than 200 ppmv in the Middle to Late Pliocene when glaciers began covering much of the Earth (Zachos et al., 2008; Breecker et al., 2009; Royer, 2010). These figures (ca. 200–1700 ppmv) bracket values known during the past ca. 65 Ma between the Late Cretaceous and the Late Pliocene. They are also those expected in the near future depending on the balance between continued CO_2 emissions and cold glacial periods of future Milankovitch cycles. For conservation purposes, it is useful to know and effectively convey to the public that these fluctuations in the concentration of greenhouse gases, along with other factors, are clearly documented in the past and that they can and have drastically altered the climates and ecosystems of the Earth: "Climatic fluctuations and vegetation responses are particularly rapid at glacial-interglacial boundaries. There is typically a gradual buildup to glacial conditions, then a precipitous and chaotic drop into interglacial climates, a process Alley (2000) likens to switches and dials. For instance, after the Last Glacial Maximum (LGM) at ca. 18,500 years BP, Greenland rapidly warmed by ca. 15°C in a decade or less at ca. 11,500 years BP, and Leyden (1984) has documented this interval of climatic instability for Guatemala" (Graham, 2010a: 267). Mean annual temperature (MAT) in the Amazon basin dropped by 5°C–6°C at the LGM ca. 21,000 years ago and was associated with extensive drying (see later section). To get a feel for what a change of 15°C, or even 5°C–6°C, means, recall press coverage in the 1980s of Midwestern farmers carrying truck-loads of hay to their drought-stricken farmers in the southeastern United States.

The rise in temperature associated with that event was 0.5°C. Relicts of former climate change are being studied to reveal how plants may persist considering the major environmental changes anticipated for the future (Hampe & Jump, 2011; Zimmer, 2011).

History is further relevant to the still-debated issue of lowland Neotropical rainforest stability (Hooghiemstra & van der Hammen, 1998). Through the 1960s, the biogeographic literature was replete with opinions suggesting that where rainforest is climax today, similar vegetation had existed uninterruptedly since a very remote geologic period; the complexity of the rainforest could be explained in terms of the seasonal and geologic stability of the climate; and in views espousing the ancient and stable environments of the tropics (Richards, 1964; Ashton, 1969). After four decades of studying the modern biota it was concluded that this presumed stability might not be true (e.g., Vuilleumier, 1971), and the fossil record has confirmed it is not. For example, at the northern limits of the modern tropical rainforest in southeastern Veracruz, Mexico, where rainforest is climax today, a Pliocene flora from a lowland area shows it was not present in the relatively recent geologic past (Graham, 1976a, 1976b). As noted previously, independent evidence from oxygen isotope and other climatological studies indicate that the MAT at the LGM was ca. 6°C lower (Webb et al., 1997) and that it was considerably drier (Maslin & Burns, 2000; Filho et al., 2002). A new study covering the last 45,000 years BP from the lowland interior of tropical South America at Laguna La Gailba near the border between Bolivia (Province Ángel Sandoval) and Brazil (Mato Grosso), hydrologically linked to the Pantanal, also reveals drying at the LGM and, by implication, at multiple times during the Quaternary: "We provide unequivocal evidence that the climate at LLG [Laguna La Gailba] was markedly drier during the last glacial period (45.0–12.2 kyr BP) than during the Holocene..." and this "strengthens the body of evidence for widespread early mid-Holocene drought across tropical South America" (Whitney et al., 2011: 177). Current droughts of even short duration have a noticeable effect on Amazonian greenness (Xu et al., 2011; Davidson et al., 2012), suggesting a prominent role for riverine dynamics in diversification (Ribas et al., 2011). It is difficult to imagine that in the 2.5 Ma of the Pleistocene, with its 18 to 20 cold/warm and moist/dry cycles, rainforest remained more or less continuously present across the Amazon basin as has been suggested (for the relevant literature see Graham, 2010a: 500–511). The historical record documents that the rainforest ecosystem is an ephemeral, delicately balanced community that has undergone significant changes in range and composition. The controversial refugium theory suggesting stability appears resolved, or at least quiescent, but its potential relevancy to conservation is clear. Too great an emphasis on stability provides a basis for the rationalization that the rainforest can be impacted with impunity and will withstand or recover because it has always done so in the past. The telling point from history is that it was not stable over long periods of time, and once it is gone, it takes intervals measured in multiple human generations and geologic time to recover.

Recent geologic history documents and provides further insight into the fluid nature of habitats, environments, and biotas. Davis (1981, 1984) long ago introduced the concept of the individual nature of species migration in response to environmental change and the availability and different distribution potentials of the propagules, the coming and going of barriers, epidemic disease, and other factors (see also Stewart et al., 2010). The consequence of this observation is that, within limits, communities of individuals, i.e., ecosystems, experience changes in composition with each environmental reshuffling. Oak-chestnut forests in the central Appalachians have included chestnut for only 2000 years. Deciduous forests in Ohio were penetrated first by hickory and then by beech 4000 years later, whereas in Connecticut, beech arrived first followed 3000 years later by hickory. Beech and hemlock entered northern hardwood forests in the Appalachians at about the same time, but hemlock arrived 2000 years before beech in New Hampshire and 2500 years before beech in upper Michigan (Davis, 1981, 1984). Beginning most recently at ca. 12,000 years ago and continuing off and on during the Holocene, there was a unique association of black ash and spruce in the upper Midwest that is no longer present today. As noted previously, an example from the tropical latitudes is the characteristic Upper Andean oak-*Weinmannia* forest that has contained oak for only the last 330,000 years, the last one eighth of the Pleistocene, because oak, although present to the north for millions of years, was able to cross into South America only after completion of the Panama land bridge, appearance of the moderate highlands, and the cooler temperatures of the Late Tertiary and Quaternary.

A recent study from Peru along the margin of the Quelcaya ice cap gives a modern patina to how changeable communities can be over relatively short periods of time with each climatic reshuffling, especially in regions with significant topographic relief. Gould et al. (2010) report that layers of vegetation about 4500 years old have been progressively uncovered since 2002 with retreat of the ice. The rate of melting is up to 60 m/yr in some places. Using the chloroplast *trnL* intron, they found fossils of at least five plants in the now dry and cold habitat at 5200 m elevation whose modern counterparts presently occur in wetlands around 4000 m. These findings suggest a community moving up-slope during earlier warm intervals, covered by ice during a cold period with components moving down-slope, the fossil remains exposed during the present warm period, and components then moving up-slope to their former habitat—all happening within the past 4500 years. The study also provides a new technique for gauging the quickening pace of change in climates and biomes (for other studies on the pace of environmental change and the biotic response, see Hampe & Jump, 2011; Clark et al., 2012; Fraser, 2012; Tingley & Huybers, 2013).

There are other implications of geohistorical data for conservation efforts and how the topic should be presented to the public. One implication is that Quaternary climatic events discovered in the high northern latitudes, and later demonstrated for the high southern latitudes, also occurred and affected the biotas of tropical regions. The Younger Dryas and Heinrich events are now being reported from Brazil and other places (see Graham, 2010a: 409–446). Another implication is that earlier concepts about the long-term, leisurely pace of these changes on scales of hundreds of thousands of years are inaccurate. In older textbooks on glacial geology, four cold periods are described alternating with three warm periods, each lasting ca. 175,000 years, for a Quaternary interval of ca. 1.2 Ma. The Quaternary is now extended back to ca. 2.5 Ma with 18 to 20 cold periods occurring on the Milankovitch eccentricity cycle of 100,000 years with other cycles of ca. 41,000 and 19,000 years. Variations in ocean circulation impose additional shorter-term cycles called Heinrich events of a few to several thousand years culminating in cold intervals, and the cool to cold Dansgaard–Oeschger events of a few thousand to several hundred years. The Younger Dryas cold event occurred between ca. 11,000 and 12,000 years ago, the mid-Holocene warm interval 6000–8000 years ago, and the Little Ice Age 1300–850 years ago, which was itself interrupted by the Medieval Warm Period 1200–800 years ago (Fagan, 2004). Many of these fluctuations are correlated with events in human history (Fagan, 1999, 2000, 2004; Alley, 2000; Flannery, 2001, 2005; Beerling, 2007). It was in the Medieval Warm Period, for example, that the Vikings were able to make their voyages of discovery to North America. In the Little Ice Age, they were forced to abandoned the settlements; Washington suffered his near-fatal winter at Valley Forge; and the citizens of London were able to walk across the solidly frozen Thames River supporting tents, shops, cafes, and small buildings. The eruption of Mount Tambora in Indonesia in 1815 (Wood, 2014) produced the following "year without a summer," during the winter of which Mary Shelley, confined to quarters near Geneva with her husband the poet Percy Shelley, Lord Byron, and others, wrote for diversion the novel *Frankenstein*. In the book, as opposed to the movie version, the prevailing cold and ice of the summer-less year play a prominent role in both the opening and closing chapters. In essence, relatively recent climate changes are being revealed as far more rapid, intense, and widespread, even in the tropics, than suspected only a few years ago.

So what is the importance of these data on near-time and deep-time history for conservation policy (Blackman et al., 2014) and the preservation of ecosystems? The fact that they are important is evident from the extensive recent literature (e.g., Balmford, 1996; Swetnam et al., 1999; Burnham, 2001; Bruzgul et al., 2005; National Research Council, 2005; Jackson & Erwin, 2006; Willis & Birks, 2006; Froyd & Willis, 2008; van Leeuwen et al., 2008; Carrasco et al., 2009; Dietl & Flessa, 2009; Keane et al., 2009; Kowalewski, 2009; Gibbons, 2010; Willis et al., 2010; Barrett et al., 2011; Robinson, 2011; Valdes, 2011; Zeebe, 2011; Gillson & Merchant, 2014). Dietl and Flessa (2011: 30; Jaramillo & Cárdenas, 2013) stress that "inclusion of geohistorical data in our decision-making process provides a more scientifically robust basis for conservation policies than those dependent on short-term observations alone." It is easily possible to convey to the public—indeed, it has been conveyed to the public—that conservation involves primarily setting aside and prohibiting access to parcels of land housing a rare, threatened (Banerjee, 2013; Cashion, 2013; Gewin, 2013; Gibson et al., 2013; Josse et al., 2013; Säterberg et al., 2013), or otherwise important species, or to a particular ecosystem, with the goal of preserving it like it is in perpetuity. Examples include stands of *Podocarpus* L'Hér. ex Pers., *Araucaria* Juss., *Nothofagus* Blume, or other vegetation types in national forests; the shrublands of *Acaena* Mutis ex L., *Polylepis* Ruiz & Pav., and *Puya* Molina and *Calamogrostis* Moench grasslands in protected areas on the páramos; and coastal regions (Harriman, 2013; Liu et al., 2013; Nature, 2013a, 2013b). If this is the impression being given, a flaw in that strategy can be claimed by those opposed to conservation efforts by citing numerous references showing that species, habitats, and ecosystems have come and gone over time. The conservation of hotspots (Joppa et al., 2011) interconnected by corridors (Robbins, 2011), monitored by remote sensing (Lucero, 2013), and inventoried through adequate and continually updated collections (Feeley & Silman, 2011) is immensely important for allowing time to collect, study (Ladle & Whittaker, 2011; Newbold, 2011), and preserve existing representatives, propagules, and DNA (Friedman, 2013; Griffith et al., 2013; Jenkins et al., 2013). Equally important are restoration efforts (Seddon et al., 2014) aimed at repairing the damage, assessing the impact of indigenous people (Luzar et al., 2012; Luzar & Fragoso, 2012; Gorenflo et al., 2012; Nature [editorial], 2012; Iwamkura et al., 2014), and, in the process, generating a better understanding of the composition, interaction, and functioning of species (Caro, 2013; Simberloff & Genovesi, 2013; Thomas, 2013) and ecosystems (Newbold, 2011; Newbold et al., 2012; Keenan et al., 2013). Additionally, however, when the dynamics of history, for example in the Anthropocene (Ruddiman, 2013), are incorporated into concepts about extant communities and publicized, a more complete, accurate, and defensible perspective of conservation and the nature of climate change (Blair et al., 2012; Clark et al., 2012; Gillis, 2013a, 2013b; Greenwald et al., 2013; Mace, 2013; Nature, 2013c, 2013d; McNutt, 2013; Tingley et al., 2013; Garcia et al., 2014) can be presented to the public; namely, that what we are actually or additionally doing is setting aside way stations. The biotas within these sites will be temporary because of both anthropogenic (Laurance, 2012a, 2012b; Laurance et al., 2012) and non-anthropogenic causes. From a geologic perspective, ecosystems of varying composition will be passing through them and at an ever-quickening pace. The essential point is that these way stations be available in the future to accommodate the new arrivals.

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